The Veliger 50(2):129–148 (June 20, 2008)

THE VELIGER
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Pliocene and Pleistocene *Fissurella* Bruguière, 1789 (Gastropoda: Fissurellidae) from Southern Peru

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Abstract. Twelve species of fossil Pliocene and Pleistocene keyhole limpets, *Fissurella* (*Fissurella*), from southern Peru are reported, including four new species: *Fissurella aranea*, sp. nov., *F. geoglypha*, sp. nov., *F. mcleani*, sp. nov., and *F. persica*, sp. nov. These species and others from Peru and Chile are assigned to several morphological species groups that are nearly congruent with clades defined by DNA sequences (Olivares, 2006). *Fissurella* (*Fissurella*) probably appeared in western South America during the late Miocene or soon thereafter, possibly from the western Pacific Ocean or South Africa, with major clades in existence in Peru by the late early Pliocene. A late Pliocene extinction of some fissurellid species and the subsequent addition of new and often larger species in Peru, Chile, and Argentina has produced the modern diverse *Fissurella* (*Fissurella*) fauna.

INTRODUCTION

In a systematic treatment of South American keyhole limpets assigned to *Fissurella* (*Fissurella*) Bruguière, 1789, McLean (1984a) lamented their limited fossil record in western South America, a record comprised only of Philippi's (1887) description of one Pliocene species from Chile, *F. concolor* Philippi, 1887, Herm's (1969) list of Pleistocene species and passing mention of Pliocene *Fissurella* from Chile, and McLean's own figures of Pliocene *F. concolor* and *Fissurella* sp., cf. *F. crassa* Lamarck, 1822, both also from Chile.

This article augments that sparse record with an account of *Fissurella* in Pliocene and Pleistocene strata from southern Peru, including the extant *F. maxima* Sowerby, 1835, *F. limbata* Sowerby, 1835, *F. crassa*, *F. latimarginata* Sowerby, 1835, and the extinct *F. concolor*, which were found in a Pliocene outcrop near the coastal town of Chala, as were two new species, *F. persica*, sp. nov., and *F. aranea*, sp. nov. A specimen of *F. pulchra* Sowerby, 1835, was found in a nearby Pliocene deposit and a worn specimen of *F. cumingi* Reeve, 1849, was discovered on a nearby middle Pleistocene marine terrace. A Pliocene exposure above the Río Acarí has yielded specimens of *F. concolor*, *F. persica*, and the extant *F. peruviana* Lamarck, 1822. Pliocene sandstones near Yauca produced single specimens of the extinct *F. mcleani*, sp. nov., and *F. geoglypha*, sp. nov. The northernmost record for any South American *Fissurella* (*Fissurella*) is formally reported, a Pliocene specimen of *F. peruviana* from northern Peru.

GEOLOGY

The Cenozoic stratigraphy of southern Peruvian forearc basins (Figure 1) was reviewed by DeVries (1998). Pliocene marine deposits of the Pisco and La Planchada formations include bioclastic sandstones and balanid coquinas (Beaudet et al., 1976; Muizon & DeVries, 1985), the remnants of littoral deposits that lapped onto pre-Eocene crystalline platforms or accumulated at the foot of steep cliffs of the Andes Cordillera.

Two outcrops of *Fissurella*-bearing Pliocene strata warrant mention. Bioclastic debris of the La Planchada Formation crops out along sweeping curves of the Panamerican Highway southeast of Chala where the road descends to the strandline at Playa Huacllaco (Figure 2). The sediments accumulated in high-energy foreshore and rocky intertidal environments in front of a rugged coastline of igneous rock (DeVries, 2003). The age of the Huacllaco beds is constrained by basal beds containing specimens of the muricid gastropods *Concholepas nodosa* Möricke, 1896, *Acanthina triangularis* DeVries, 2003, and *Herminespina mirabilis* (Möricke, 1896), which collectively indicate a late early to early late Pliocene age (DeVries & Frassinetti, 2003), and by the uppermost and oldest marine terrace, whose elevation and largely extant taxa, including *Acanthina unicornis* (Bruguière, 1789) and *Concholepas concholepas* (Bruguière, 1789), suggest a latest Pliocene age (Muizon & DeVries, 1985; DeVries, 1995, 2000, 2003). Four lithologic units were designated in the Huacllaco section: Unit I (crossbedded balanid coquina, late early Pliocene), Unit II (bioclastic sandstone and polychaete reefs, late early or early late Pliocene), Unit III (ferruginous cobble-bearing bioclastic sandstone, early late Pliocene), and Unit IV (conglomerates and massive coquina beds, late late Pliocene).

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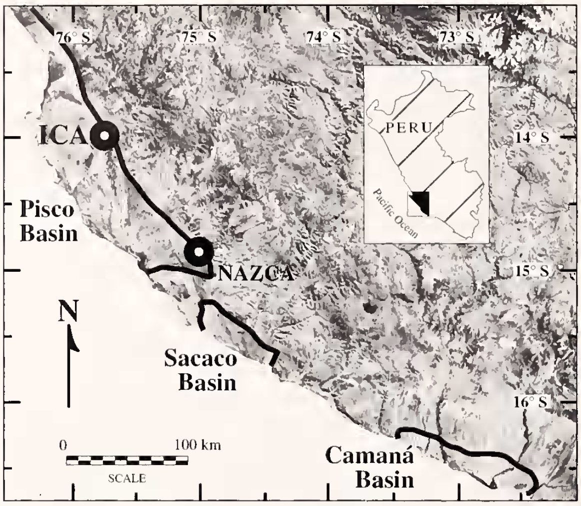


Figure 1. Location of forearc basins (Pisco, Sacaco, Camaná) along the coast of southern Peru.

The second notable outcrop lies east of Chauviña, set back from the southeastern rim of the Río Acarí, where small knobs of bedded strata constitute a condensed section of lower Pliocene to uppermost Pliocene bioclastic sandstone and coquina (Figure 3). The Acarí section has a basal lag of igneous boulders with mollusks (*Herminespina saskiae* DeVries & Vermeij, 1997, *Trophon carlosmartini* DeVries, 2005, and *Xanthochorus ochuroma* DeVries, 2005) that indicate an early Pliocene age (DeVries & Vermeij, 1997; DeVries, 2005a, 2005b). Beds five and six meters above the boulders contain *Concholepas kieneri* Hupé, 1854, and *Anadara* aff. *A. chilensis* (Philippi, 1887), as well as the aforementioned muricids, collectively indicating a somewhat later early Pliocene age (Muizon & DeVries, 1985; DeVries, 1995, 2000). Beds nine and 11 m above the boulders with *Concholepas camerata* DeVries, 2000, *Stramonita chocolata* (Duclos, 1832), *Xanthochorus xuster* DeVries, 2005, and *Xanthochorus cassidiformis* (Blainville, 1832), indicate a late Pliocene age (DeVries, 2000, 2005a, 2007). An overwhelming preponderance of extant molluscan taxa (e.g., *Concholepas concholepas* and *Xanthochorus cassidiformis*) in the uppermost coquinas, coinciding with the most elevated and oldest marine terrace, indicate a latest Pliocene age (Muizon & DeVries, 1985).

MATERIALS AND METHODS

Specimens of fossil *Fissurella* described in this study were found by the author. Most fossil examples had lost their aragonitic inner layer, so features of the external calcitic layer (shape, radial and concentric sculpture, ray patterns, margin width and coloration) became the principal means for diagnosing species, with greatest emphasis placed on radial sculpture.

Comparative fissurellid material came from the Natural History Museum of Los Angeles County (LACM) and the author's personal collection. Selected citations are given for known species, emphasizing those that post-date McLean (1984a).

Locality and sample descriptions are listed in the appendix. Lengths (L), widths (W) and heights (H) are measured in millimeters. Dimensions of broken specimens are enclosed by parentheses. Some figured specimens are coated with ammonium chloride; others are shown with transmitted light to reveal color patterns. Types and other numbered specimens are deposited at the University of Washington's Burke Museum of Natural History and Culture in Seattle, Washington (UWBM), the Departamento de Paleontología de Vertebrados, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, in Lima, Peru (MUSM INV) and in the case of one specimen of *Fissurella peruviana*, the Orton Geological Museum, The Ohio State University (OSU).

SYSTEMATIC PALEONTOLOGY

Family Fissurellidae Fleming, 1822

Subfamily Fissurellinae Fleming, 1822

Genus *Fissurella* Bruguière, 1789

Subgenus *Fissurella* Bruguière, 1789

Type species (by monotypy) *Patella nimbosa* Linnaeus, 1758. Recent, Caribbean.

Discussion: McLean (1984a) included within *Fissurella* (*Fissurella*) all fissurellid gastropods with an aragonitic inner shell layer and calcitic outer shell layer, i.e., 13 South American taxa and two species from the northern hemisphere, *F.* (*Fissurella*) *volcano* Reeve, 1849 (California), and *F.* (*Fissurella*) *nimbosa* (Linnaeus, 1758) (Caribbean Sea, Brazil). Stuber (1991) supported the monophyly of *Fissurella* (*Fissurella*) *sensu* McLean (1984a), but Olivares (2006) did not, concluding instead that molecular data showed *F. nimbosa* to be more closely related to the eastern Atlantic *F.* (*Cremides*) *schrammi* Fischer, 1857, than South American species of *Fissurella* (*Fissurella*). Until molecular data become available for *F. volcano*, McLean's (1984a) definition of *Fissurella* (*Fissurella*) will be utilized here, with the caveat that removing both *F. volcano* and *F. nimbosa* from the subgenus would result in a South American subset of *Fissurella* equivalent to Pérez-Farfante's (1943) imperfectly diagnosed *Fissurella* (*Balboaina*).

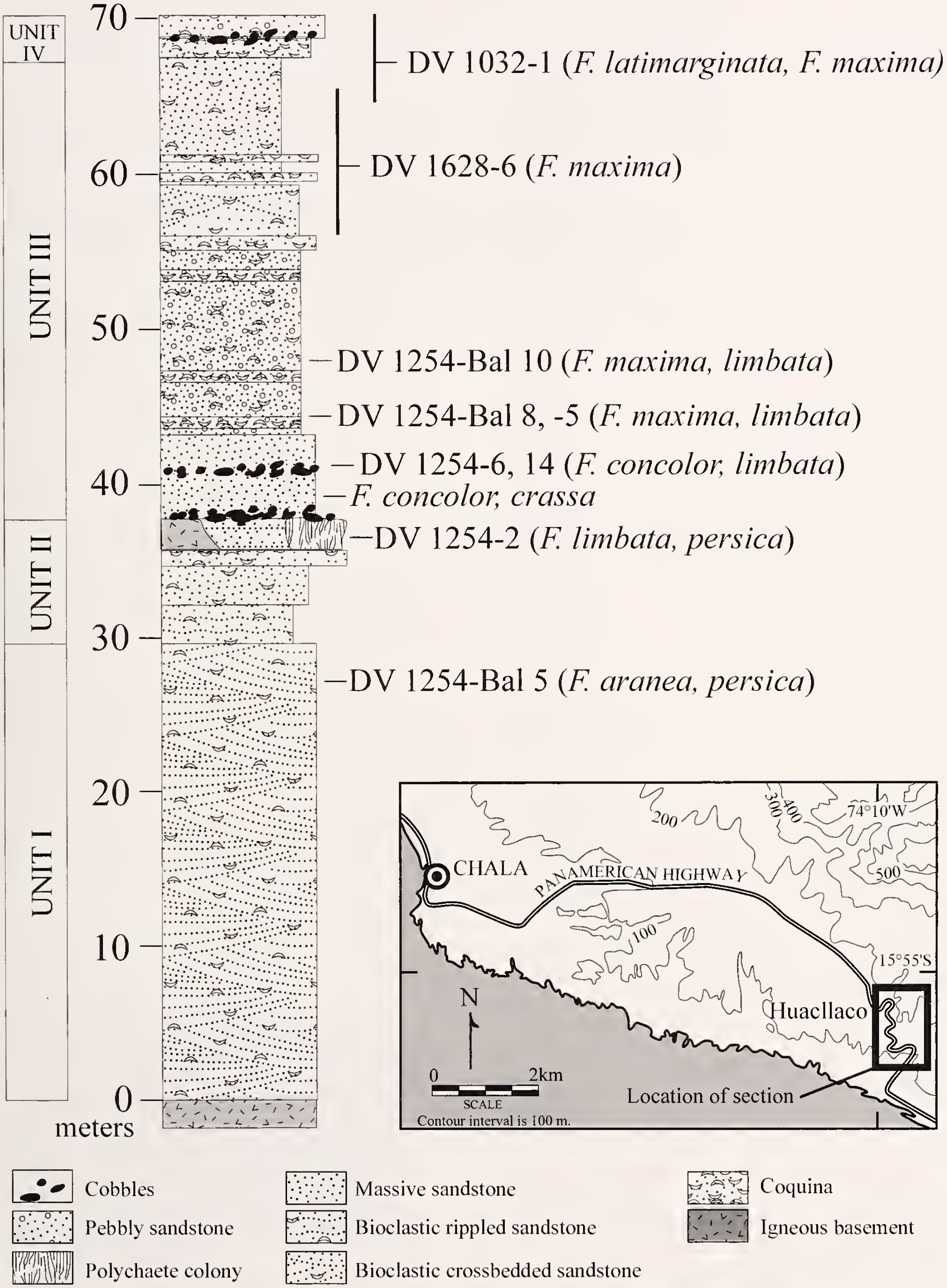
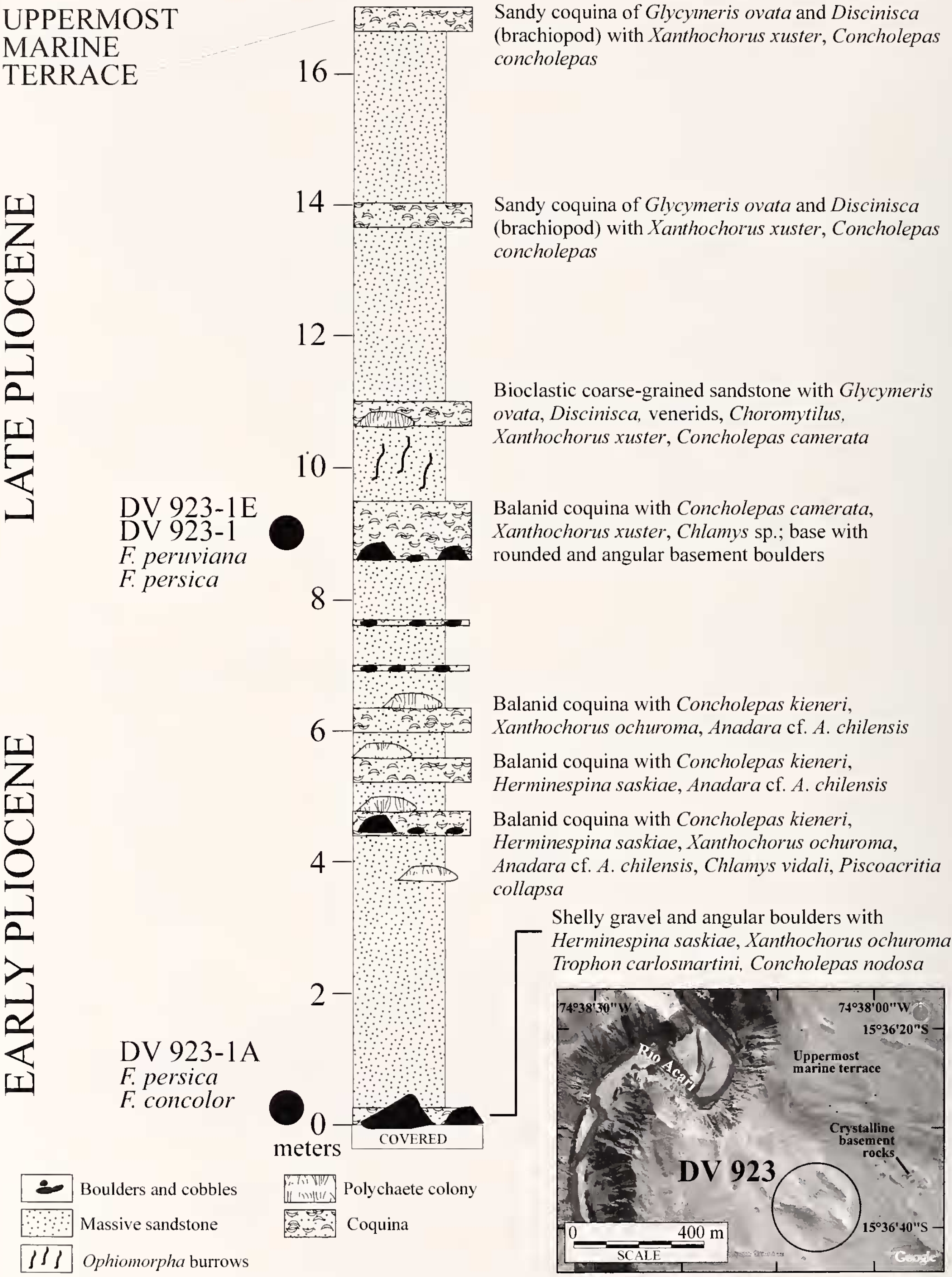

UNIT IV
UNIT III
UNIT II
UNIT I
70
60
50
40
30
20
10
0
meters
DV 1032-1 (F. latimarginata, F. maxima)
DV 1628-6 (F. maxima)
DV 1254-Bal 10 (F. maxima, limbata)
DV 1254-Bal 8, -5 (F. maxima, limbata)
DV 1254-6, 14 (F. concolor, limbata)
F. concolor, crassa
DV 1254-2 (F. limbata, persica)
DV 1254-Bal 5 (F. aranea, persica)
CHALA
PANAMERICAN HIGHWAY
200
300
400
500
100
74°10'W
15°55'S
Huacllaco
N
0
2km
SCALE
Contour interval is 100 m.
Location of section
Cobbles
Pebbly sandstone
Polychaete colony
Massive sandstone
Bioclastic rippled sandstone
Bioclastic crossbedded sandstone
Coquina
Igneous basement

Figure 2. The Huacllaco lithologic section southeast of Chala, type locality of *Fissurella aranea*, sp. nov. The location map is shown in inset.



Sandy coquina of *Glycymeris ovata* and *Discinisca* (brachiopod) with *Xanthochorus xuster*, *Concholepas concholepas*

Sandy coquina of *Glycymeris ovata* and *Discinisca* (brachiopod) with *Xanthochorus xuster*, *Concholepas concholepas*

Bioclastic coarse-grained sandstone with *Glycymeris ovata*, *Discinisca*, venerids, *Choromytilus*, *Xanthochorus xuster*, *Concholepas camerata*

Balanid coquina with *Concholepas camerata*, *Xanthochorus xuster*, *Chlamys* sp.; base with rounded and angular basement boulders

Balanid coquina with *Concholepas kieneri*, *Xanthochorus ochuroma*, *Anadara* cf. *A. chilensis*

Balanid coquina with *Concholepas kieneri*, *Herminespina saskiae*, *Anadara* cf. *A. chilensis*

Balanid coquina with *Concholepas kieneri*, *Herminespina saskiae*, *Xanthochorus ochuroma*, *Anadara* cf. *A. chilensis*, *Chlamys vidali*, *Piscoacritia collapsa*

Shelly gravel and angular boulders with *Herminespina saskiae*, *Xanthochorus ochuroma*, *Trophon carlosmartini*, *Concholepas nodosa*

Figure 3. Lithologic section at the Acarí site southeast of the Río Acarí, type locality (DV 923) for *Fissurella persica*, sp. nov. The location map is shown in inset. Associated mollusks listed in section are discussed in DeVries (2000, 2003, 2005a, 2005b), DeVries & Hess (2004), and DeVries & Vermeij (1997).

Fissurella (*Fissurella*) *maxima* Sowerby, 1835

Figures 4–10, 17, 18

Fissurella maxima Sowerby, 1835a, p. 123.
Fissurella maxima Sowerby, 1835b, p. 3, fig. 18.
Fissurella maxima Sowerby, 1835. McLean, 1984a, p. 25, figs. 51–63.
Fissurella maxima Sowerby, 1835. Oliva & Castilla, 1992, p. 92, fig. 4.
Fissurella maxima Sowerby. Alamo & Valdivieso, 1997, p. 7, fig. 12.
Fissurella maxima Sowerby, 1835. Guzmán et al., 1998, p. 29, with figure.
Fissurella maxima Sowerby, 1834 [*sic*]. Forcelli, 2000, p. 48, fig. 23.

Diagnosis: Shell large. Ribs strong, wide, well differentiated by size, corrugated to imbricate. Purplish rays broad. Margin coarsely crenulated. Rays penetrate entire calcitic layer.

Discussion: Small specimens with characters of *Fissurella maxima*, including coloration, were found in bioclastic sandstones in the upper part of the Huacllaco section (Figure 2) and assigned a late Pliocene age based on the presence of associated molluscan taxa [*Prisogaster valenciai* DeVries, 2006, *Acanthina unicornis*, *Chorus* transitional between *C. giganteus* (Lesson, 1830) and *C. grandis* (Philippi, 1887), *Concholepas camerata*, *Xanthochorus xuster* (DeVries 1997, 2000, 2003, 2005a, 2006)].

Two Peruvian specimens of *Fissurella maxima* exhibit oval external scars from the epibiotic limpet, *Scurria variabilis* (Sowerby, 1839) [= *Scurria parasitica* (Orbigny, 1841); see Espoz et al., 2004] (Figure 8). Such scars are most often found on Recent specimens of *F. crassa* and *F. limbata* (Figures 22, 35).

Material: MUSM INV 164, DV 401-1, Recent, L 44.4, W 30.9, H 10.1; MUSM INV 165, DV 1032-1, late Pliocene, L 37.6, W 27.5, H 7.7; UWBM 98437, Lomas, Recent, L 87.7, W 59.4, H 22.0; UWBM 98438, Lomas, L 75.9, W 48.7, H 17.5; UWBM 98439, Lomas, L 55.3, W 36.9, H 13.2; UWBM 98440, Lomas, L 51.6, W 31.7, H 10.6; UWBM 98441, DV 1372-1, Recent, L 60.3, W 35.8, H 13.7; UWBM 98442, DV 1372-1, L 65.7, W 42.8, H 14.7; UWBM 98443, DV 1628-6, late Pliocene, L 43.5, W 29.3, H 10.6; UWBM 98444, DV 1254-Ball0, late Pliocene, L 16.3, W 10.4, H 4.5; UWBM 98482, DV 1418-1, late Pliocene, L 32.6, W 21.5, H 5.3; UWBM 98483, DV 1418-1, L (12.6).

Occurrence: Late Pliocene: southern Peru. Pleistocene: central Chile. Recent: north-central Peru to central Chile.

Fissurella (*Fissurella*) *concolor* Philippi, 1887

Figures 11–16, 19

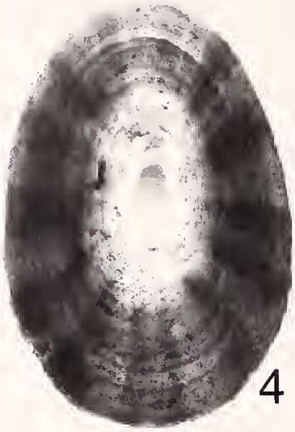
Fissurella concolor Philippi, 1887, p. 98, pl. 58, fig. 8.
Fissurella concolor Philippi, 1887. McLean, 1984a, p. 15, fig. 17.

Diagnosis: Shell medium-sized, elongate, tapered. Ribs strong, well differentiated by size, weakly corrugate or smooth. Margin moderately wide, coarsely crenulated.

Description: Shell length up to 60 mm, elongate, strongly tapered anteriorly. Height low. Sides of shell elevated. Ribs prominent, sharply rounded, smooth to slightly imbricate, differentiated into primary ribs, some bifurcated, usually with three intervening secondary ribs, the medial being stronger; smaller specimens with one intervening secondary rib between primary ribs. Margin moderately wide, crenulated by ribs. Rays narrow, purplish, generally coinciding with primary ribs; anterior rays weak or absent. Aragonitic inner layer missing. Foramen anterior to center, shape unknown.

Discussion: *Fissurella concolor* was first described from Pliocene beds near Mejillones, Chile by Philippi (1887) and figured again by McLean (1984a). Peruvian specimens, like those from Chile, are elongate and have ribs that are more sharply raised and less imbricate than those on specimens of *F. maxima*. The oldest example from Peru came from the lowest boulder bed of the Acarí locality (DV 923-1a) together with *F. persica*, sp. nov., and mollusks indicating an early Pliocene age [*Acanthina triangularis* DeVries, 2003, *Concholepas nodosa*, *C. kieneri*, and *Herminespina saskiae* (DeVries, 1995, 2000, 2003; DeVries & Vermeij, 1997)]. Other specimens were found in the lowest cobble-rich bioclastic sandstone in the Huacllaco section (DV 1254-14); associated mollusks (*Acanthina* transitional between *A. triangularis* and *A. unicornis*; *Concholepas camerata*; *Xanthochorus xuster*) indicate an early late Pliocene age. Higher in the Huacllaco section the only strongly ribbed *Fissurella* specimens are referable to *F. maxima*.

Material: MUSM INV 171, DV 1032-2, early late Pliocene, L 35.9, W 22.1, H 7.0; MUSM INV 172, Huacllaco, early late Pliocene, L (26.2), W 16.9, H 5.9; MUSM INV 173, DV 1254-14, early late Pliocene, L 28.0, W 16.4, H 3.3; UWBM 98463, DV 923-1a, early Pliocene, L (11.1), W 9.1, H 2.0; UWBM 98464, Huacllaco, late Pliocene, L 47.9, W 29.1, H 10.8; UWBM 98465, DV 1032-2, L 24.5, W 14.5, H 5.2; UWBM 98466, DV 1032-2, L 19.6, W 16.9, H (5.1); UWBM 98467, DV 1254-6, late Pliocene, L 19.3, W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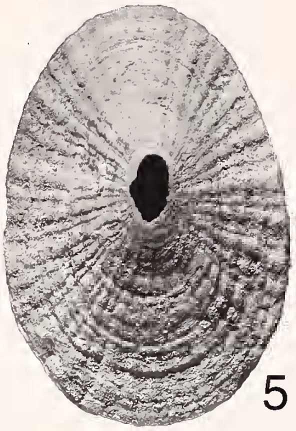
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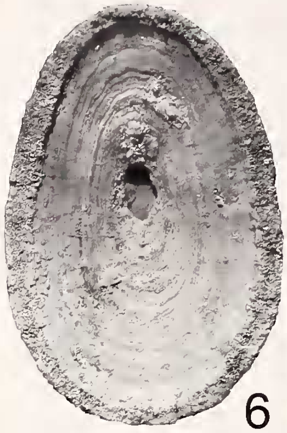
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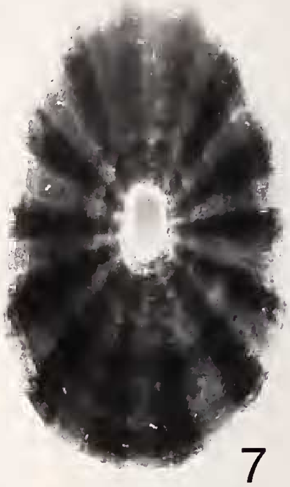
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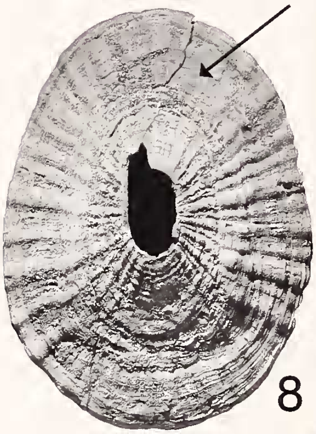
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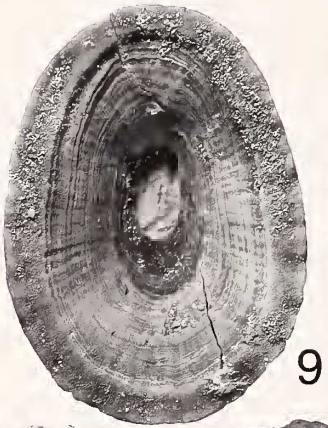
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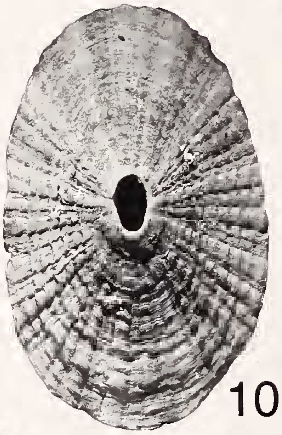
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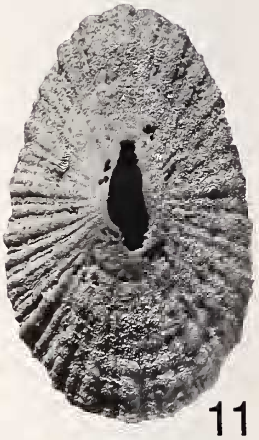
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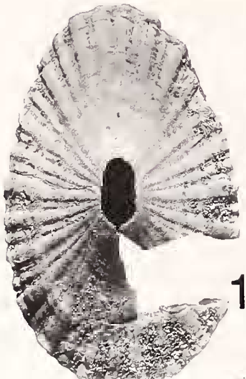
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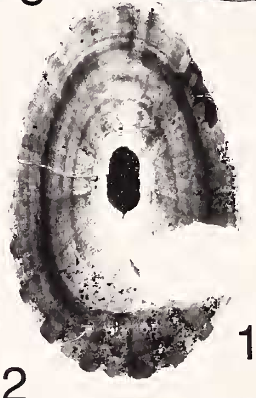
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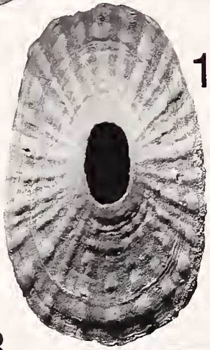
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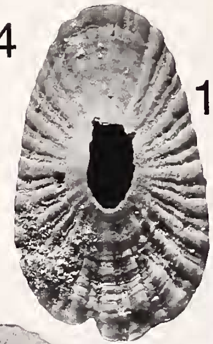
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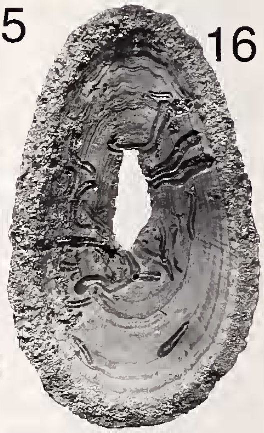
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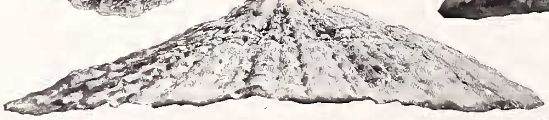
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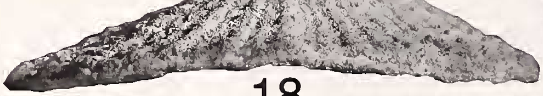
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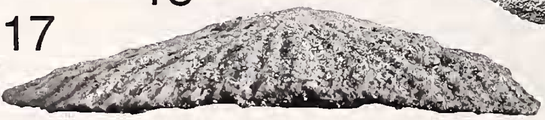
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Figures 4–10, 17, 18. *Fissurella* (*Fissurella*) maxima Sowerby, 1835.
Figure 4. UWBM 98443, DV 1628-6. Late Pliocene. Transmitted light showing rays. Length is 43.5 mm.
Figure 5. UWBM 98443. Dorsal view.
Figure 6. UWBM 98443. Ventral view, aragonitic inner layer missing.
Figure 7. UWBM 98441, DV 1372-1. Recent. Transmitted light showing rays. Length is 60.3 mm.

11.5, H 4.1; UWBM 98468, DV 1254-14, L 29.6, W 18.4, H 3.9; UWBM 98469, DV 1254-14, L (37.9).

Occurrence: Early to early late Pliocene: southern Peru. Pliocene: north-central Chile.

Fissurella (*Fissurella*) *aranea*, sp. nov.

Figures 20, 21, 34

Diagnosis: Shell small, elongate-quadrate. Height low. Ribs sharply defined, alternating primary and secondary. Margin wide.

Description: Shell small, less than 30 mm long, elongate-quadrate, slightly tapered anteriorly. Height low. Ends slightly raised. Sculpture of well defined, closely spaced, narrow ribs, alternatingly primary and secondary; moderately imbricate at intersections with strong growth lines. No coloring preserved. Margin wide, irregularly scalloped. Foramen probably slightly anterior to center.

Discussion: Specimens of *Fissurella aranea* differ from contemporaneous small specimens of *F. persica*, sp. nov., by being more quadrate and having ribs that alternate regularly in size, in contrast with fine equally sized ribs on specimens of *F. persica*. Ribs on specimens of *F. concolor* and *F. maxima* are coarser and alternate less regularly.

Etymology: Latin noun ‘aranea,’ meaning ‘spider net,’ referring to the intersecting ribs and concentric growth lines on this species.

Type Locality: DV 1254, section along Panamerican Highway above Playa Huacllaco, 27 m in measured section (see Appendix).

Material: UWBM 98479, DV 1254-Bal5, holotype, late early Pliocene; L 27.4, W 16.7, H (4.9); UWBM 98480, DV 923-1e, early late Pliocene, L (17.9), W 13.2, H (2.7).

Occurrence: Late early Pliocene to early late Pliocene: southern Peru.

Fissurella (*Fissurella*) *limbata* Sowerby, 1835

Figures 22–33

Fissurella limbata Sowerby, 1835a, p. 123.
Fissurella limbata Sowerby, 1835b, p. 3, figs. 42, 66, 74.
Fissurella limbata Sowerby, 1835. McLean, 1984a, p. 55, figs. 212–224.
Fissurella limbata Sowerby, 1835. Oliva & Castilla, 1992, p. 7, fig. 10.
Fissurella limbata Sowerby. Alamo & Valdivieso, 1997, p. 93, fig. 10.
Fissurella limbata Sowerby, 1835. Guzmán et al., 1998, p. 28, with figure.
Fissurella limbata Sowerby, 1835. Forcelli, 2000, p. 49, fig. 25.

Diagnosis: Shell medium-sized. Ribs broad, subdued, some with weak secondary ribs; ribs often obsolete towards foramen. Margin wide. Calcitic outer layer with translucent veneer.

Discussion: Modern specimens of *Fissurella limbata* have ribs that are less well defined than those of *F. maxima*. Such specimens were encountered in bioclastic sandstones in the upper half of the Huacllaco section near Chala (DV 1254-14), together with specimens of *F. concolor*. One specimen (Figure 27) has a nearly full suite of primary, secondary, and tertiary ribs extending to the foramen, such as is seen on specimens of *F. maxima*, although the ribs are subdued and lack the imbricate texture of the latter species. Rays are seen to penetrate the entire calcitic outer layer, but perhaps only because the purple color of the flattened margin is faded.

Associated mollusks indicate a late Pliocene age. Not one Pliocene specimen exhibited the external scar of the epibiotic limpet, *Scurria variabilis*, which is commonly seen on modern specimens of *F. limbata* (Figures 22, 29).

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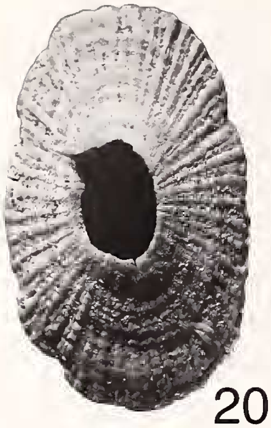
Figure 8. MUSM INV 165, DV 1032-1. Late Pliocene. Dorsal view; arrow marks scar from *Scurria* limpet. Length is 37.6 mm.
Figure 9. MUSM INV 165, ventral view.
Figure 10. UWBM 98440, Lomas. Recent. Dorsal view. Length is 51.6 mm.
Figure 17. UWBM 98443, lateral view, anterior to right.
Figure 18. UWBM 98441, lateral view, anterior to right.
Figures 11–16, 19. *Fissurella* (*Fissurella*) *concolor* Philippi, 1887.
Figure 11. UWBM 98464, Huacllaco. Early late Pliocene. Dorsal view. Length is 47.9 mm.
Figure 12. MUSM INV 171, DV 1032-2. Late early Pliocene. Dorsal view. Length is 35.9 mm.
Figure 13. MUSM INV 171, transmitted light.
Figure 14. UWBM 98465, DV 1032-2. Early late Pliocene. Dorsal view. Length is 24.5 mm.
Figure 15. MUSM INV 173, DV 1254-14. Early late Pliocene. Dorsal view. Length is 28.0 mm.
Figure 16. UWBM 98464, ventral view.
Figure 19. UWBM 98464, lateral view, anterior to right.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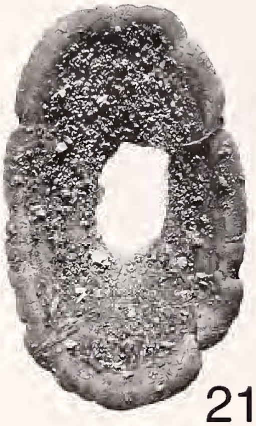
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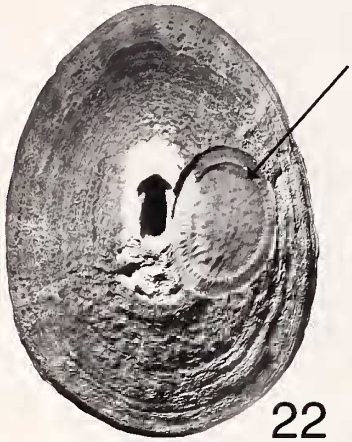
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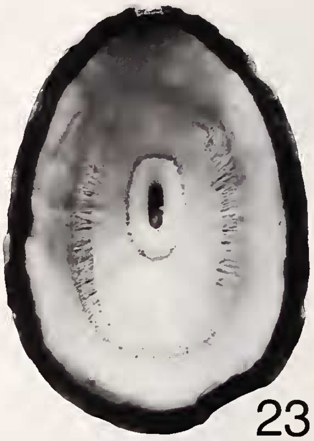
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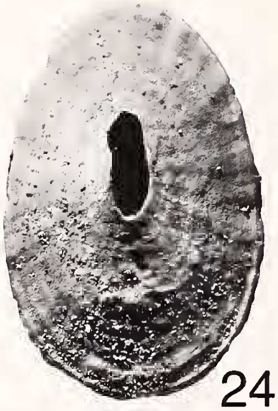
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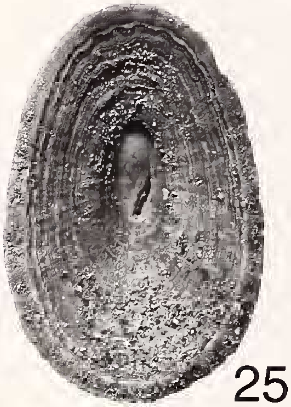
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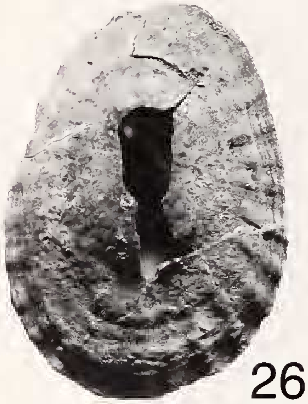
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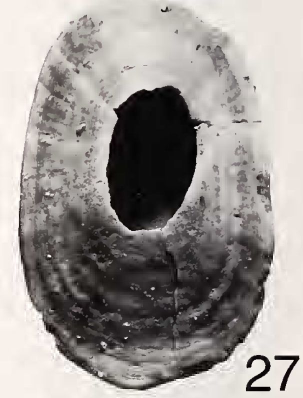
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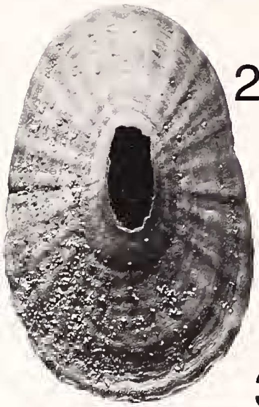
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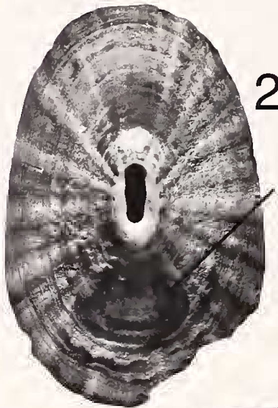
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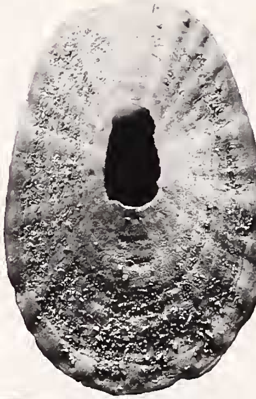
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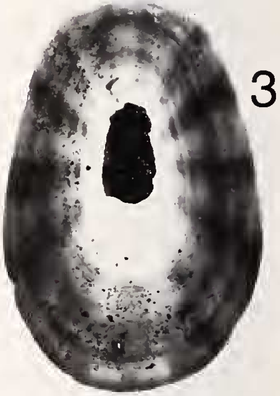
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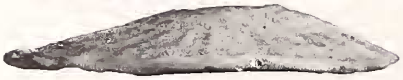

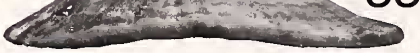
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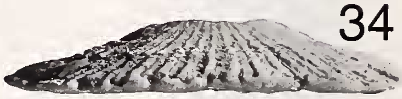


Figures 20, 21, 34. *Fissurella* (*Fissurella*) *aranea*, sp. nov. UWBM 98479, DV 1254-Bal5. Holotype. Late early Pliocene. Length is 27.4 mm.

Figure 20. Dorsal view.

Figure 21. Ventral view.

Figure 34. Lateral view, anterior to right.

Figures 22–33. *Fissurella* (*Fissurella*) *limbata* Sowerby, 1835.

Figure 22. MUSM INV 167, DV 810-1. Holocene. Dorsal view. Length is 60.8 mm. Arrow marks scar from *Scurria* limpet.

Figure 23. MUSM INV 167, ventral view.

Figure 24. MUSM INV 170, Hucallaco. Early late Pliocene. Dorsal view. Length is 37.6 mm.

Figure 25. MUSM INV 170, ventral view.

Material: MUSM INV 163, DV 1372-1, Recent, L 63.4, W 43.7, H 15.3; MUSM INV 167, DV 810-1, Holocene, L 60.8, W 43.6, H 18.7; MUSM INV 168, DV 1254-5, late Pliocene, L 62.8, W 42.1, H 17.0; MUSM INV 169, DV 1254-14, early late Pliocene, L (28.5); MUSM INV 170, lowest Huacllaco cobbles, 37 m, early late Pliocene, L 37.6, W 24.9, H 6.5; UWBM 98452, Lomas, Recent, L 50.4, W 33.7, H 12.9; UWBM 98453, Lomas, L 48.8, W 33.6, H 11.9; UWBM 98454, DV 810-1, L 72.2, W 49.8, H 18.8; UWBM 98455, DV 1254-6, late Pliocene, L 53.9, W 37.5, H (15); UWBM 98456, DV 1254-14, L 42.6, W 30.1, H 11.3; UWBM 98460, DV 1254-10, late Pliocene, L 36.4, W 24.4, H 8.2; UWBM 98461, DV 1254-14, L 34.6, W 21.9, H 6.2; UWBM 98462, DV 1254-14, L 36.6, W 23.9, H 8.7; UWBM 98457, DV 1372-1, L 36.9, W 23.9, H 9.0; UWBM 98458, DV 1372-1, L 38.6, W 25.9, H 8.9; UWBM 98459, DV 1372-1, L (22.9), W 16.8, H 7.0; UWBM 98478, DV 1254-2, early late Pliocene, L (27.7).

Occurrence: Late Pliocene: southern Peru. Recent: north-central Peru to Chiloé, Chile.

Fissurella (*Fissurella*) *crassa* Lamarck, 1822

Figures 35–37

Fissurella crassa Lamarck, 1822, 6(2), p. 11.
Fissurella crassa Lamarck, 1822. Sowerby, 1835b, p. 1, figs. 9, 11.
Fissurella crassa Lamarck, 1822. McLean, 1984a, p. 58, figs. 225–237.
Fissurella crassa Lamarck, 1822. Oliva & Castilla, 1992, p. 92, fig. 5.
Fissurella crassa Lamarck. Alamo & Valdivieso, 1997, p. 6, fig. 11.
Fissurella crassa Lamarck, 1822. Guzmán et al., 1998, p. 27, with figure.
Fissurella crassa Lamarck, 1822. Forcelli, 200, p. 46, fig. 13.

Diagnosis: Shell medium-sized to large, elongate, with upturned ends and margins; margin with fimbriate edge. Ribs and rays poorly developed. Foramen elongate.

Discussion: Specimens of *Fissurella crassa* are more elongate and less tapered than those of *F. limbata* and have nearly obsolete ribs. A fragment of *Fissurella* from the lower half of the Huacllaco section (Figure 37) has the same uniquely scalloped, fimbriate, upturned margin as specimens of extant *F. crassa* and so is referred to this species.

Material: MUSM INV 166, DV 810-1, Holocene, L 61.1, W 36.3, H 13.3; UWBM 98447, DV 1372-1, Recent, L 63.6, W 35.9, H 14.7; UWBM 98448, Lomas, Recent, L 52.3, W 31.1, H 11.3; UWBM 98449, Lomas, L 42.6, W 24.1, H 9.6; UWBM 98450, DV 810-1, L 62.8, W 39.6, H 15.4; UWBM 98451, Huacllaco, 39 m, early late Pliocene, L (19.7).

Occurrence: Early late Pliocene: southern Peru. Late Pliocene: Chile. Recent: north-central Peru to Chiloé, Chile.

Fissurella (*Fissurella*) *peruviana* Lamarck, 1822

Figures 38–42

Fissurella peruviana Lamarck, 1822, p. 15.
Fissurella peruviana Lamarck, 1822. McLean, 1984a, p. 21, figs. 31–50.
Fissurella peruviana Lamarck, 1822. Alamo & Valdivieso, 1997, p. 7, fig. 13.
Fissurella peruviana Lamarck, 1822. Guzmán et al., 1998, p. 29, with figure.
Fissurella peruviana Lamarck, 1822. Forcelli, 2000, p. 48, fig. 22.

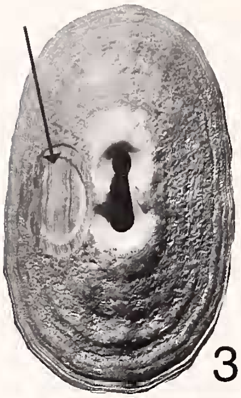
Diagnosis: Shell small, profile high. Fine primary and secondary ribs. Color usually charcoal gray; rays obscured. Margin narrow. Foramen small, oval.

Discussion: Specimens with the high conic shell and fine ribs of *Fissurella peruviana* were found in a coquina bed nine meters above the valley floor of the Acarí outcrop (Figure 3). Associated mollusks (*Concholepas camerata*, *Xanthochorus xuster*, *Stramonita chocolata*) indicate a late Pliocene age (DeVries, 2000, 2005a, 2007).

A specimen (OSU 38157) assigned herein to *Fissurella peruviana* was found in the gravel-rich cross-bedded sandstones of the basal Taime Formation in northern Peru (DV 239-11; DeVries, 1986, 1988).

←

Figure 26. UWBM 98456, DV 1254-14. Early late Pliocene. Dorsal view. Length is 42.6 mm.
Figure 27. UWBM 98462, DV 1254-14. Dorsal view. Length is 36.6 mm.
Figure 28. UWBM 98461, DV 1254-14. Dorsal view. Length is 34.6 mm.
Figure 29. UWBM 98457, DV 1372-1. Recent. Dorsal view. Length is 36.9 mm. Arrow marks scar from *Scurria* limpet.
Figure 30. UWBM 98460, DV 1254-10. Late Pliocene. Dorsal view. Length is 36.4 mm.
Figure 31. UWBM 98460, transmitted light showing rays.
Figure 32. UWBM 98461, lateral view, anterior is to right.
Figure 33. UWBM 98462, lateral view, anterior is to left.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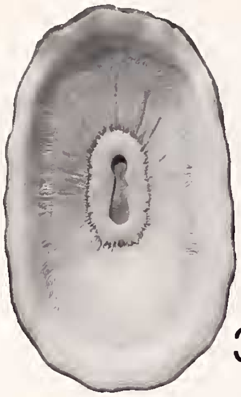
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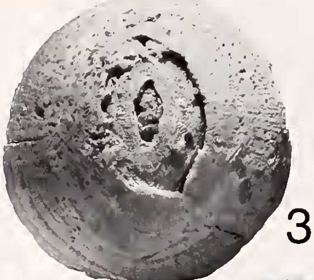
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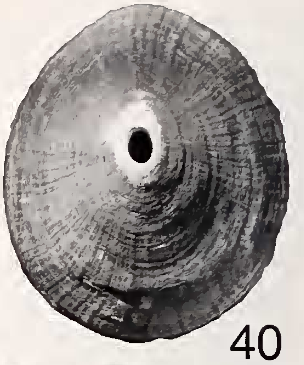
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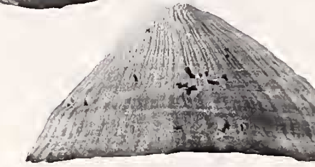
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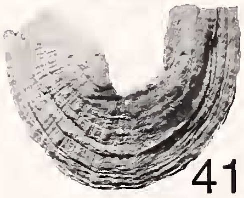
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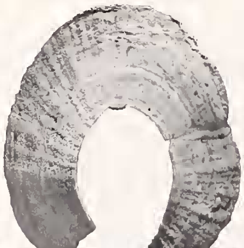
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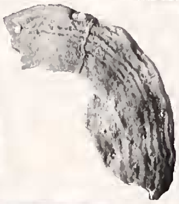
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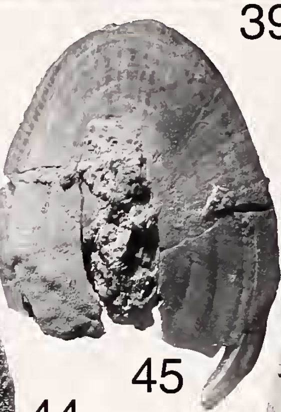
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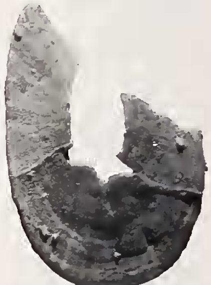
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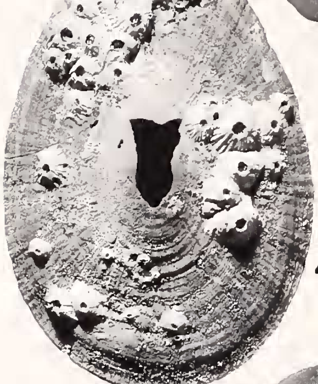
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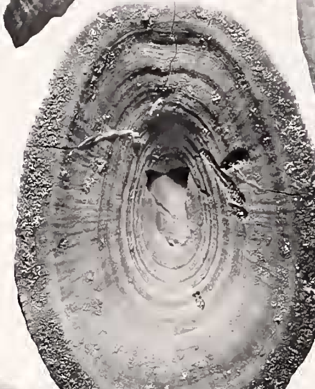
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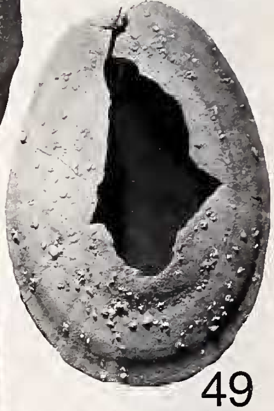
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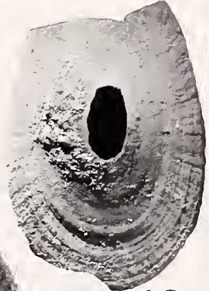
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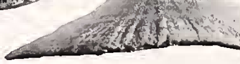
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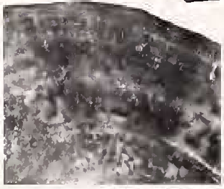
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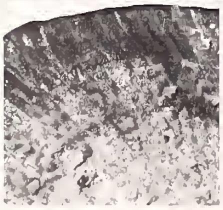
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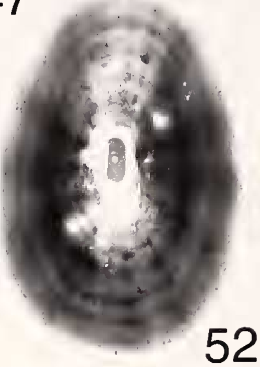
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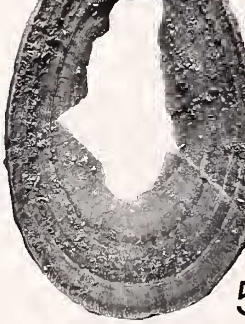
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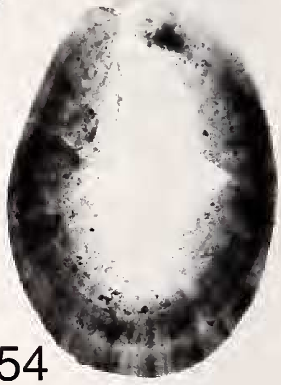
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Figures 35–37. *Fissurella* (*Fissurella*) *crassa* Lamarck, 1822.
Figure 35. MUSM INV 166, DV 810-1. Holocene. Dorsal view. Length is 61.1 mm. Arrow marks scar from *Scurria* limpet.
Figure 36. MUSM INV 166, ventral view.
Figure 37. UWBM 98451, Huacllaco. Early late Pliocene. Dorsal view of fragment. Length is 19.7 mm.
Figures 38–42. *Fissurella* (*Fissurella*) *peruviana* Lamarck, 1822.

The elongate foramen differs from the oval foramen seen on southern Peruvian and Chilean specimens (Figure 38) but the size and arrangement of radial ribs are identical, as is the high conic profile.

Material: MUSM INV 161, DV 923-1e, early late Pliocene, L (25.3); MUSM INV 162, DV 923-1, early late Pliocene, L (26.0), W 21.5, H (7.4); OSU 38157, DV 239-11, late Pliocene, L 21.4, W 20.7, H 10.8; UWBM 98424, DV 1141-1, Recent, L 40.3, W 34.2, H 16.5; UWBM 98425, DV 1141-1, L 33.4, W 23.9, H 15.4; UWBM 98426, La Mina, Recent, L 33.4, W 24.9, H 12.6; UWBM 98427, DV 599-2, middle Pleistocene, L 31.0, W 22.5, H 10.2; UWBM 98428, DV 1141-1, L 19.9, W 13.8, H 9.3; UWBM 98429, DV 401-1, Recent, lot of 2; UWBM 98430, DV 923-1e, early late Pliocene, L (20.6), W 25.3, H 10.4.

Occurrence: Early late Pliocene: northern to southern Peru. Recent: north-central Peru to south-central Chile.

Fissurella (*Fissurella*) *latimarginata* Sowerby, 1835

Figures 43, 44, 47, 48

Fissurella latimarginata Sowerby, 1835a, p. 126.
Fissurella latimarginata Sowerby, 1835b, p. 3, fig. 69.
Fissurella latimarginata Sowerby, 1835. McLean, 1984a, p. 28, figs. 64–79.
Fissurella latimarginata Sowerby, 1835. Oliva & Castilla, 1992, p. 92, fig. 6.
Fissurella latimarginata Sowerby. Alamo & Valdivieso, 1997, p. 6.
Fissurella latimarginata Sowerby, 1835. Guzmán et al., 1998, p. 28, with figure.
Fissurella latimarginata Sowerby, 1835. Forcelli, 1835, p. 46, fig. 12.

Diagnosis: Shell large, height low to moderate. Color charcoal gray. Ribs fine, poorly differentiated; rays usually obscured. Margin wide. Foramen elongate.

Discussion: A specimen of *Fissurella latimarginata* (Figure 43) was found in the upper part of Unit III of the Huacllaco section (Figure 2), together with the transitional *Chorus giganteus*/*C. grandis* and *Concholepas camerata*, both indicative of a late Pliocene age. Another specimen of *F. latimarginata* was found at Quebrada Champeque (DV 1251-1), 10 m above basement rocks and 10 m below the uppermost marine terrace, together with *Concholepas camerata*, *Xanthochorus xuster*, and *Acanthina unicornis*, which collectively indicate a late Pliocene age (DeVries, 2000, 2003, 2005a).

Material: MUSM INV 163, DV 1251-1, late Pliocene, L (27.9), 19.2, H 7.8; UWBM 98433, DV 1032-1, late Pliocene, L 49.5, W 35.6, H 9.1; UWBM 98434, DV 1372-1, Recent, L 55.6, W 37.2, H 13.2; UWBM 98435, Lomas, Recent, L 69.5, W 50.2, H 16.4; UWBM 98436, Lomas, 53.5, W 37.5, H 11.8.

Occurrence: Late Pliocene: southern Peru. Recent: north-central Peru to central Chile.

Fissurella cumingi Reeve, 1849

Fissurella cumingi Reeve, 1849, pl. 3, fig. 17.
Fissurella cumingi Reeve, 1849. Hupé, 1854, p. 238.
Fissurella cumingi Reeve, 1849. McLean, 1984a, p. 31, figs. 80–94.
Fissurella cumingi Reeve, 1849. Oliva & Castilla, 1992, p. 92, fig. 7.
Fissurella cumingi Reeve, 1849. Guzmán et al., 1998, p. 27, with figure.

←

Figure 38. OSU 38157, DV 239-11. Late Pliocene. Dorsal view. Length is 21.4 mm.
Figure 39. UWBM 98424, DV 1141-1. Recent. Dorsal view. Length is 40.3 mm.
Figure 40. UWBM 98424, lateral view, anterior is to left.
Figure 41. UWBM 98430, DV 923-1e. Early late Pliocene. Dorsal view of fragment. Length is 20.6 mm.
Figure 42. MUSM INV 162, DV 923-1. Early late Pliocene. Dorsal view of fragment. Length is 26.0 mm.
Figures 43, 44, 47, 48. *Fissurella* (*Fissurella*) *latimarginata* Sowerby, 1835.
Figure 43. UWBM 98433, DV 1032-1. Late Pliocene. Dorsal view. Length is 49.5 mm.
Figure 44. UWBM 98433, ventral view.
Figure 47. MUSM INV 163, DV 1251-1. Late Pliocene. Dorsal view. Length is 27.9 mm.
Figure 48. MUSM INV 163, lateral view, anterior is to right.
Figures 45, 46. *Fissurella* (*Fissurella*) *persica* sp. nov.
Figure 45. UWBM 98470, DV 923-1a, holotype. Early Pliocene. Dorsal view. Length is 31.9 mm.
Figure 46. UWBM 98477, DV 1254-Bal5. Late early Pliocene. Dorsal view. Length is 20.5 mm.
Figures 49–54. *Fissurella* (*Fissurella*) *pulchra* Sowerby, 1835.
Figure 49. UWBM 98432, DV 1251-1. Late Pliocene. Dorsal view. Length is 52.6 mm.
Figure 50. LACM 75-31 a, Chile. Recent. Close-up showing unique mottling.
Figure 51. UWBM 98432, close-up showing unique mottling.
Figure 52. LACM 75-31 b, Chile. Recent. Transmitted light showing acicular rays.
Figure 53. UWBM 98432, ventral view.
Figure 54. UWBM 98432, transmitted light showing acicular rays.

Fissurella cumingi Reeve, 1849. Forcelli, 2000, p. 48, fig. 24.

Diagnosis: Shell large, light colored, with fine ribs and well-defined rays.

Discussion: A large broken and worn specimen of *Fissurella cumingi* was found on a middle Pleistocene terrace (elevation 160 m above sea level) north of Chala. A large modern specimen from Lomas is very similar to the Pleistocene specimen.

Material: LACM 75-32, Chile, Recent, lot of 31; UWBM 98445, DV 465-1, middle Pleistocene, L (59.3), W 55.0, H 20.3; UWBM 98446, Lomas, Recent, L 77.3, W 55.7, H 25.3.

Occurrence: Early middle Pleistocene: southern Peru. Recent: southern Peru to south-central Chile.

Fissurella (*Fissurella*) *persica*, sp. nov.

Figures 45, 46

Diagnosis: Shell small, height low. Ribs fine, weak, generally undifferentiated. Rays broad, forming a suffusion of purple-peach color in transmitted light.

Description: Shell small, length less than 40 mm. Oval, sharply tapered anteriorly. Height low. Calcitic outer layer thin. Sculpture of numerous thin ribs; ribs equally sized, barely raised, differentiated in anterior quadrant only. Ground color cream; broad rays of purplish-peach color. Margin flat, narrow, coloring of rays passes through entire thickness of outer layer. Foramen not preserved, probably just anterior to center.

Discussion: Specimens of *Fissurella persica* closely resemble those of the opaquely gray *F. latimarginata* with their fine ribs and sharply tapered anterior. They are lighter colored, however, like specimens of *F. cumingi*, with visible rays and a narrow margin. Their ribs are more uniformly sized than those of both *F. latimarginata* and *F. cumingi*.

The holotype of *Fissurella persica* was found in bioclastic gravel near the base of the Acarí outcrop (Figure 3). Its occurrence with *Trophon carlosmartini*, *Herminespina saskiae*, and *Xanthochorus ochuroma* indicates an early Pliocene age. Fragments of *F. persica* were also found in the upper bioclastic sandstones of the Acarí locality (early late Pliocene) and Unit I of the Huacllaco outcrop (late early Pliocene).

Etymology: Latin noun '*persica*,' meaning 'peach,' for the purple-peach color of the species' rays under transmitted light.

Type Locality: DV 923, knobs southeast of the Río Acarí, east of Chauviña (Figure 3; see Appendix).

Material: MUSM INV 174, DV 923-1, early late Pliocene, L (12.9); MUSM INV 175, DV 923-1, L (17.5); UWBM 98431, DV 923-1, early late Pliocene, L (21.8); UWBM 98470, DV 923-1a, early Pliocene, holotype, L (31.9), W 25.0, H 7.2; UWBM 98471, DV 1254-Bal5, late early Pliocene, L (25.4); UWBM 98472, DV 923-1e, early late Pliocene, L (27.3); UWBM 98473, DV 923-1e, L (29.5); UWBM 98476, DV 1254-2, early late Pliocene, L 22.7, W 15.4, H 2.8; UWBM 98477, DV 1254-Bal5, (20.5), W 14.4, H 3.4.

Occurrence: Early to early late Pliocene: southern Peru.

Fissurella (*Fissurella*) *pulchra* Sowerby, 1835

Figures 49–54

Fissurella pulchra Sowerby, 1835a, p. 124.
Fissurella pulchra Sowerby, 1835b, p. 3, fig. 24.
Fissurella pulchra Sowerby, 1835. McLean, 1984a, p. 63, figs. 254–267.
Fissurella pulchra Sowerby, 1835. Oliva & Castilla, 1992, p. 93, fig. 11.
Fissurella pulchra Sowerby, 1835. Guzmán et al., 1998, p. 30, with figure.
Fissurella pulchra Sowerby, 1835. Forcelli, 2000, p. 49, fig. 27.

Diagnosis: Shell medium-sized, smooth. Height very low. Surface with purple-and-white streaky mottling. Broad rays superimposed on irregularly spaced acicular rays.

Discussion: A single specimen of *Fissurella pulchra*, distinguished by its exterior mottling and smooth surface, was discovered in late Pliocene deposits north of Chala. Both modern and fossil examples have weakly developed ribs anteriorly.

Material: LACM 75-31, Recent, Chile, lot of 10; UWBM 98432, DV 1251-1, L 52.6, W 36.0, H 8.4.

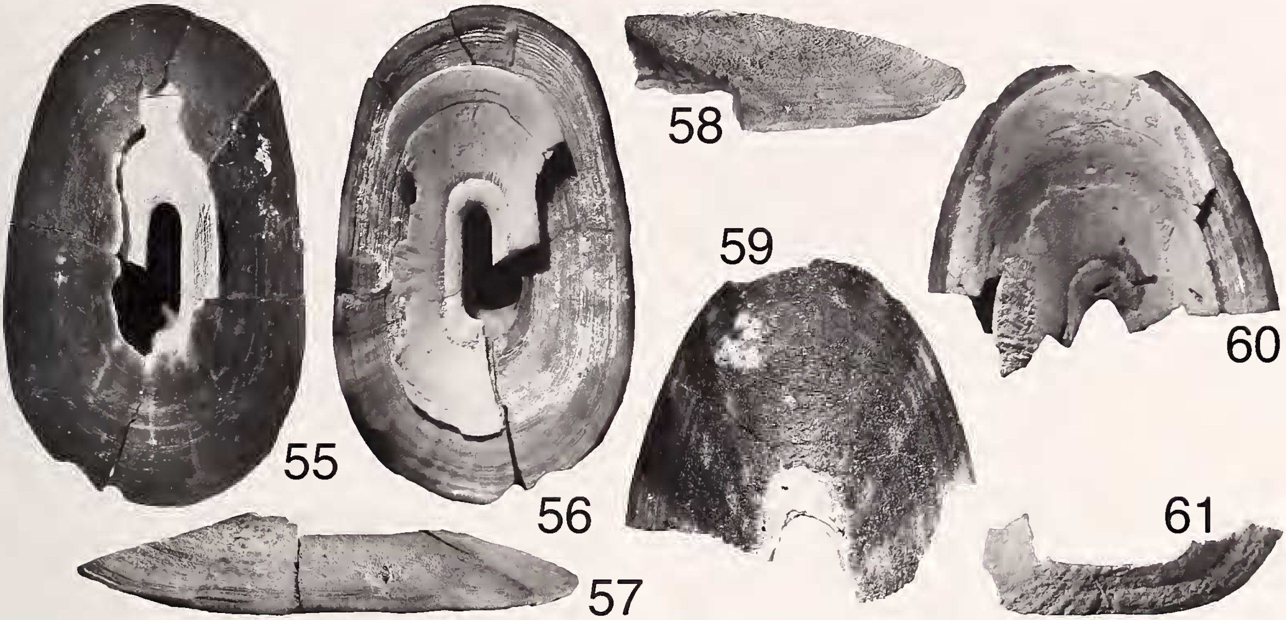
Occurrence: Late Pliocene: southern Peru. Recent: north-central Peru to central Chile.

Fissurella (*Fissurella*) *mcleani*, sp. nov.

Figures 55–57

Diagnosis: Shell medium-sized, elongate. Exterior black, smooth. Foramen exceptionally elongate. Ends elevated.

Description: Shell medium-sized, length almost 60 mm, elongate, tapered slightly anteriorly; ends of shell elevated. Height low. Surface black, smooth, with rare radial wrinkles marking edges of obsolete radial ribs. Numerous thin reddish rays, only visible, barely,



Figures 55–57. *Fissurella* (*Fissurella*) *mcleani*, sp. nov. UWBM 98475, DV 1635-2. Holotype. Early Pliocene. Length is 58.4 mm.
Figure 55. Dorsal view.
Figure 56. Ventral view showing partial layer of aragonite and very elongate foramen.
Figure 57. Lateral view, anterior to right.
Figures 58–60. *Fissurella* (*Fissurella*) *geoglypha*, sp. nov. UWBM 98474, Yauca. Holotype. Early Pliocene. Length is 35.0 mm.
Figure 58. Lateral view, anterior to right.
Figure 59. Dorsal view.
Figure 60. Ventral view, showing partial layer of aragonite.
Figure 61. *Diodora* sp. UWBM 98481, DV 923-1a. Early Pliocene. Dorsal view of fragment; note squared off posterior to left. Length is 18.4 mm.

apically. Margin moderately wide, smooth, with broad obsolete rays producing alternating cream and black-colored intervals. Aragonite layer partially preserved. Foramen situated slightly posteriorly; exceptionally elongate, without constrictions.

Discussion: *Fissurella* (*Fissurella*) *mcleani* has an exceptionally elongate foramen and a smooth black surface. Specimens of *Fissurella pulchra* are equally smooth, but possess a normally elongate foramen and lack the deep black color of *F. mcleani*.

Associated mollusks from the same beds (*Anadara* cf. *A. chilensis*, *Acanthina obesa* DeVries, 2003, *Concholepas kieneri*, *Herminespina saskiae*, *Xanthochorus ochuroma*) at locality DV 1635-1 indicate an early Pliocene age; the presence of *X. eripepomus* DeVries, 2005, further suggests a late early Pliocene age.

Etymology: Named in recognition of James H. McLean (Natural History Museum of Los Angeles County) and his studies on *Fissurella* (*Fissurella*).

Type Locality: DV 1635, Yauca depression, west of Panamerican Highway, northwest of Yauca (Figure 62; see Appendix).

Material: UWBM 98475, DV 1635-2, holotype, late early Pliocene, L 58.4, W 32.6, H 13.3.

Occurrence: Late early Pliocene: southern Peru.

Fissurella (*Fissurella*) *geoglypha*, sp. nov.

Figures 58–60

Diagnosis: Shell medium-sized, smooth. Exterior black; cream-colored rays sharply defined, broad.

Description: Shell with estimated length of 60 mm, anterior strongly tapered, posterior unknown. Height low. Anterior end of shell elevated. Exterior smooth. Rays sharply defined, broad, penetrate calcitic outer layer. Margin rounded, moderately wide. Aragonitic shell layer partially preserved.

Discussion: The holotype of *Fissurella geoglypha* is more bowed than the smooth flat specimens of *F. pulchra* and lacks the latter's characteristic mottling; it is also less quadrate than the holotype of *F. mcleani*, which lacks any broad rays. Associated mollusks from the Yauca roadcut (*Anadara* cf. *A. chilensis*, *Concho-*

lepas nodosa, *Xanthochorus ochuroma*) indicate an early Pliocene age (DeVries, 2000, 2005a).

Etymology: Named for radiating geoglyphs that are part of the pre-Columbian Nazca lines in southern Peru.

Type Locality: Yauca, roadcut in Panamerican Highway on north side of Río Yauca (Figure 62; see Appendix).

Material: UWBM 98475, Yauca, holotype, late early Pliocene, L (35.0), W (36.5), H 12.1.

Occurrence: Late early Pliocene: southern Peru.

DISCUSSION

There is no consensus regarding the grouping of related species within *Fissurella* (*Fissurella*). Pilsbry (1890) recognized four species groups based on shell morphology, whereas McLean (1984a) defined three groups according to the relative thickness of the aragonitic inner and calcitic outer layers. Stuber (1991) utilized 34 anatomical, radular, and morphological characters to produce a cladogram for 26 extinct and extant fissurellid taxa. She recognized a primitive clade comprising *F. peruviana* and the two extralimital northern hemisphere species (*F. nimbosa*, *F. volcano*), a polytomous clade that included South American and South African species with well developed ribs, and a clade with smooth-shelled, weakly ribbed, and finely ribbed taxa.

The ensuing description of new morphological groups of *Fissurella* (*Fissurella*) is informed by a consideration of species' temporal ranges but is based largely on shell sculpture. These new groups are compared with clades derived from an analysis of molecular data by Olivares (2006).

Groups of related *Fissurella* (*Fissurella*) species

Coarsely ribbed group: *Fissurella maxima*, *F. costata*, and *F. picta* have long been considered closely related because of their similar coarse radial sculpture (Pilsbry, 1890; McLean, 1984a; Stuber, 1991). All three species occur in Pleistocene deposits of Chile (Herm, 1969); *F. picta* is also found on Pleistocene marine terraces in Argentina (Aguirre et al., 2005). Of the three taxa, the only Peruvian species, *F. maxima*, occurs in the upper part of Unit III at Huacllaco (Figure 2), but not in *Fissurella*-bearing beds of Unit II or the lower part of Unit III, suggesting that the species may have first appeared following the early late Pliocene. Other coarsely ribbed species (*F. concolor*, *F. aranea*) extend the record of this group back to the early Pliocene.

'limbata' lineage: Specimens of *Fissurella limbata* have low, broad, and sometimes obsolete ribs and few secondary ribs. The oldest examples are found in upper Unit II beds at Huacllaco. Some Huacllaco specimens have ribs nearly as well differentiated as those on specimens of late Pliocene *F. maxima* (compare Figure 28 with Figure 8), suggesting that *F. limbata* diverged from the coarsely ribbed group during the late early Pliocene.

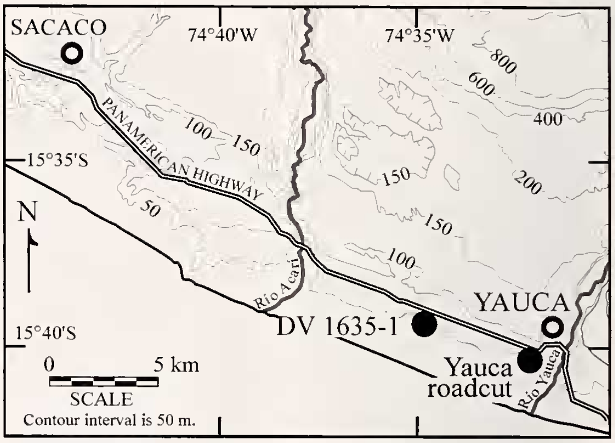


Figure 62. Type localities of *Fissurella mcleani*, sp. nov. (DV 1635-1) and *F. geoglypha*, sp. nov. (Yauca roadcut).

Finely ribbed group: The fossil record of *F. latimarginata* (late Pliocene to Recent) and *F. persica* (early Pliocene) shows that finely ribbed species have long constituted a distinct morphological group. *Fissurella peruviana*, another species with fine ribs, appeared first during the early late Pliocene (Figure 3), suggesting it is more deeply rooted within the group than *F. latimarginata*. Less deeply rooted may be *F. cumingi*, an extant species greatly resembling *F. latimarginata* that was found on an early middle Pleistocene marine terrace.

Smooth-shelled group: A single specimen of *Fissurella pulchra* (Figure 49) was found in upper Pliocene deposits of southern Peru. The discovery of two new late early Pliocene smooth-shelled species, *F. mcleani* (Figure 55) and *F. geoglypha* (Figure 59), shows that this group was well established as early as the other morphological groups.

'crassa' lineage: The fimbriate wrinkle-ribbed *Fissurella crassa* occurs in early late Pliocene deposits of southern Peru (Figure 2), as well as Pliocene beds in Chile (McLean, 1984a). Its unusual blunt anterior and weakly developed and widely spaced primary ribs crossing an otherwise smooth surface makes its assignment to other groups problematic.

Unassigned taxa: Some species of *Fissurella* (*Fissurella*) are difficult to assign to an existing morphological group. *Fissurella radiosa* Lesson, 1831, a late Pleistocene to Recent species from southern Chile and Argentina, might be placed with finely ribbed taxa, although its narrow ribs are sharply elevated. The extant *F. bridgesii* Reeve, 1849, from Peru and Chile, is irregularly striated and ribbed and might belong with finely ribbed taxa. *F. nigra* Lesson, 1831, a large extant species from southern Chile, has fine striations and is not clearly a member of any group.

To summarize: data from western South America point to the existence of at least five fissurellid groups with fossil and modern constituents (Figure 63): a coarsely ribbed group (*F. aranea*, *F. concolor*, *F. maxima*, *F. picta*, *F. costata*), a 'limbata' lineage (*F. limbata*), a finely ribbed group (*F. persica*, *F. peruviana*, *F. latimarginata*, *F. cumingi*, *F. oriens* Sowerby, 1835, *F. bridgesii*), a 'crassa' lineage (*F. crassa*), and a smooth-shelled group (*F. mcleani*, *F. geoglypha*, *F. pulchra*). The differentiated ribs on some fossil specimens of *F. limbata* suggest the 'limbata' lineage and the coarsely ribbed group (*F. maxima* and others) share a common early Pliocene ancestor. All morphological groups were already established by the late early Pliocene, implying their common ancestor probably existed no more recently than the earliest Pliocene. To date, however, *Fissurella* of such antiquity have not been found in southern Peru.

Comparison with Molecular Data

Olivares (2006) sequenced partial nucleotide sequences of several mitochondrial and nuclear genes from all 13 of McLean's (1984a) extant South American species of *Fissurella* (*Fissurella*), as well as the extant Caribbean *F. nimbosa* and extant eastern Atlantic *F. schrammi* and *Diodora graeca* (Linnaeus, 1758). His molecular phylogeny, which is remarkably congruent with the phylogeny hinted at by the paleontological data, includes:

a. a coarsely ribbed clade that includes *F. maxima* + *F. limbata*,
b. a deeply rooted clade with finely ribbed taxa, including *F. latimarginata* + *F. cumingi*, and a sister group composed of *F. pulchra* + *F. radiosa*,
c. a deeply rooted *F. peruviana* that is a sister taxon to other finely ribbed species, and
d. a deeply rooted *F. crassa* with uncertain clade affinities.

The most significant incongruency between the molecular and morphological species groupings is the placement of *Fissurella radiosa*. That the broad, low, smooth-shelled *F. pulchra* and elongate, high-crowned, sharply ribbed *F. radiosa* could be sister species (Olivares, 2006) is startling. Yet, every tree-producing algorithm presented Olivares with the same *pulchra* + *radiosa* group, no matter which DNA sequence was used. In the case of randomly amplified polymorphic DNA (RAPD) data analyzed using the UPGMA method (unweighted pair group method with arithmetic mean), however, *F. radiosa* was grouped with *F. crassa* and *F. nigra* in a deeply rooted clade (Olivares, 2006). The discrepant phylogenetic results for *F. radiosa* remain unexplained.

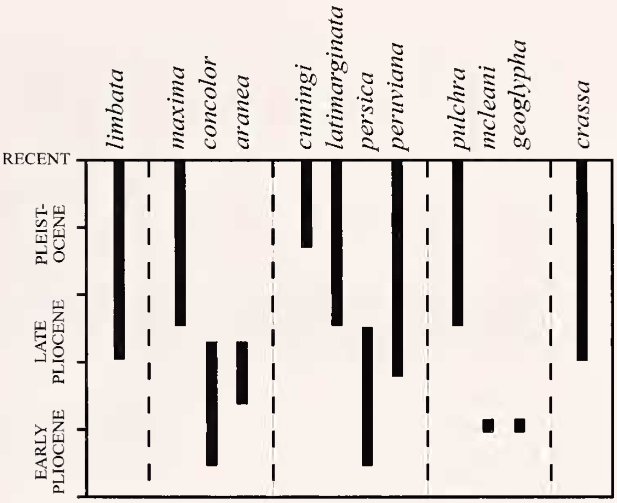


Figure 63. Estimates of temporal ranges for species of *Fissurella* (*Fissurella*) found in southern Peru.

Molecular ages for branching within the *Fissurella* (*Fissurella*) clade of Olivares (2006) are consistently younger compared with ages inferred from paleontological data (Table I). The discrepancies may be due in part to an age estimate for the uppermost terrace in southern Peru (2 Ma) that is too old or molecular calibration points that are too young (e.g., Pleistocene ages for the first appearance of *F. maxima* and *F. peruviana*).

Diversity Patterns

The species richness of Chilean and Peruvian fissurellid faunas for the Pliocene and Quaternary is summarized in Table II. Species richness appears to have increased during the Quaternary, a trend contrary to that for the rest of the Peruvian molluscan fauna (DeVries, 1995, 1997, 2001, 2003). Alternatively, fissurellids may simply be poorly preserved in older deposits. Extinct species of *Fissurella* are found only in Pliocene beds, not in Pleistocene deposits, in agreement with diversity patterns for the entire Pliocene-Quaternary molluscan fauna of western South America, which suffered a major species-level extinction during the late Pliocene (Herm, 1969; DeVries, 1985, 2001; Rivadeneira & Marquet, 2007).

Large species of *Fissurella* (>80 mm maximum length) appear only in Quaternary deposits (Table III). In contrast, the oldest species of *Fissurella* (*F. aranea*, *F. persica*) are among the smallest species (maximum length < 40 mm).

Origin of South American *Fissurella*

Fissurella (*Fissurella*) is notable for its taxonomic diversity in western South America since the early Pliocene and complete lack of a fossil record beforehand, even though upper Miocene littoral deposits are common in southern Peru (DeVries, 1998). Miocene Fissurellidae have been identified in Chile (Tavera, 1979; Nielsen, 2003), but the two new taxa illustrated by Nielsen (2003) are probably examples of *Diodora* Gray, 1821. The holotype of *Fissurella alternula* Tavera, 1979, might also be a *Diodora* (Tavera, 1979, 1991); other early Miocene species of *Diodora* are known from Chile (Nielsen, 2003) and an early Pliocene specimen has been found in southern Peru (Figure 61). South American *Fissurella* (*Fissurella*) most likely did not originate from early Miocene Chilean limpets.

If *Fissurella* was introduced to western South America, the avenues for introduction were few: immigration from (1) the Caribbean Sea or eastern North Pacific Ocean by way of northwestern South America, (2) the western Pacific Ocean or Indian Ocean by means of the high latitude West Wind Drift or equatorial countercurrents, or (3) the South Atlantic Ocean. Plausible examples exist for the first two scenarios, e.g., (1) the muricid, *Pterorytis* Conrad, 1862, arriving in southern Peru from the North Pacific Ocean during the early late Pliocene (DeVries, 2005c), and (2) the turbinid ancestor of *Prisogaster* Mörch, 1850, arriving from the western Pacific Ocean during the middle to late Miocene (DeVries, 2006). No persuasive examples of the third scenario are known (Nielsen, personal communication, 2007).

The occurrence of *Fissurella peruviana* in the Taime Formation of northern Peru (DeVries, 1986, 1988) could be construed as evidence for a Pliocene connection with northern hemisphere fissurellids (*F. nimbosa*, *F. volcano*) involving either emigration of Caribbean fissurellids southward (Olivares, 2006) or Peruvian taxa northward (Stuber, 1991). The anomalous presence of other higher latitude species in the Taime Formation, however, suggests that a northward expansion of the Peruvian Faunal Province during the late Pliocene (DeVries, 1986) would best explain the odd occurrence of *F. peruviana* near the Equator. No other species of *Fissurella* (*Fissurella*) have been found in Miocene or Pliocene beds in northern Peru or Ecuador (e.g., Olsson, 1932, 1964; Pilsbry & Olsson, 1941; Marks, 1951; DeVries, 1986). Absent such a record, passage of diverse *Fissurella* populations during the Pliocene through northwestern South America from the Caribbean seems unlikely. The emigration of *Fissurella* from Peru to California, however, resulting

Table I

Ages for cladogenetic events affecting *Fissurella* (*Fissurella*). See Olivares (2006) for molecular data and basis for estimating ages. Paleontological ages are estimates based on faunal correlations with a radiometrically dated section at Sacaco (Muizon & DeVries, 1985) that also yielded biostratigraphically useful diatoms (H. Schrader, written communication, 1986) and a 2-Ma age for the uppermost uplifted marine terrace in southern Peru.

Event	Molecular age (Ma)	Paleontological age (Ma)
Basal polytomy for *Fissurella* (*Fissurella*)	3.5–2.14	>4
Divergence of *F. limbata* and ancestor of *F. maxima*	2.18–1.3	>2.3
Fissurella latimarginata species complex polytomy, including divergence of *F. latimarginata* and *F. cumingi*	0.2–0.12	>1.4

Table II

Species numbers of western South American *Fissurella* (*Fissurella*) for different time intervals since the early Pliocene. Data from Herm (1969), McLean (1984) and this report.

Time interval	Species list for chile, peru	Number of species
Recent	*bridgesii, costata, crassa, cumingi, latimarginata, limbata, maxima, nigra, oriens, peruviana, picta, pulchra, radiosa*	13
Pleistocene	*costata, crassa, cumingi, latimarginata, limbata, maxima, peruviana, picta, pulchra*	9
Late late Pliocene	*crassa, latimarginata, limbata, maxima, peruviana, pulchra*	6
Early late Pliocene	*concolor, crassa, limbata, persica, peruviana*	5
Early Pliocene	*aranea, concolor, geoglypha, mcleani, persica*	5

Table III

Maximum of sizes of *Fissurella* (*Fissurella*) species through time. Data from McLean (1984) and fossils described in this paper. Large species (maximum length > 80 mm) are shaded black; medium sized species (maximum length 40–80 mm) are shaded medium gray; and small species (maximum length < 40 mm) are shaded light gray.

	persica	*aranea*	*concolor*	*mcleani*	*geoglypha*	*peruviana*	*crassa*	*limbata*	*latimarginata*	*pulchra*	*maxima*	*cumingi*	*costata*	*picta*	*bridgesii*	*oriens*	*radiosa*	*nigra*
Recent						░	■	■	■	▨	■	■	▨	■	■	▨	▨	■
Pleistocene						░						■						
Late late Pliocene						░	▨	▨	▨	▨	▨							
Early late Pliocene	░	░	▨			░	▨	▨										
Early Pliocene	░	░	░	▨	▨													

in the Pleistocene establishment (Grant & Gale, 1931) of a single species, *F. volcano*, as proposed by Stuber (1991), cannot be ruled out.

The first species of *Fissurella* (*Fissurella*) probably arrived in Chile or Peru during the late Miocene or earliest Pliocene, since the subgenus was fully diversified by the late early Pliocene. In southern Peru, late Miocene antecedents to the modern Peruvian molluscan fauna were already established following a major species-level extinction event between 14 and 11 Ma (DeVries, 2001, 2002; DeVries & Frassinetti, 2003). Late Miocene rocky intertidal and mixed rock-and-sand subtidal molluscan faunas included numerous muricid genera and teguline trochids, as well as barnacles and the inarticulate brachiopod, *Discinisca* Dall, 1871 (DeVries, 1995, 1997, 2003, 2005a, 2005b). To this mix were added the turbinid, *Prisogaster* (about 10 Ma), the trochinine trochid, *Piscoacritia* DeVries and Hess, 2004 (about 7 Ma), and a thaid, *Purpura boliviana* Philippi, 1887 (about 7 Ma), all probably with western Pacific ancestry (DeVries and Hess, 2004; DeVries, 2006; DeVries, unpublished data). Fissurellids from the western Pacific Ocean or Indian Ocean could have arrived similarly. Other keyhole limpets (*Fissurellidea* group of genera) do show a disjunct South African and southern South American distribution (McLean, 1984b), which lends credence to a Southern Ocean origin for South American *Fissurella* (*Fissurella*).

The difficulty with a western Pacific or South African origin for South American *Fissurella* is that no obvious candidate for an ancestor exists. *Monodilepas monilifera* (Hutton, 1873), a New Zealand limpet with an early Miocene to Recent record (Dell, 1953; Beu & Maxwell, 1990), has a very broad foramen, cancellate sculpture, and lacks an aragonite/calcite shell structure. The same is true for some South African fissurellids [*Fissurellidea aperta* (Sowerby, 1825)]. Other South African fissurellids, including the coarsely ribbed modern *Fissurella mutabilis* Sowerby, 1834, and finely ribbed *F. natalensis* Krauss, 1848, as well as the smooth-shelled fossil *F. robusta* Sowerby, 1889, and *F. glarea* Carrington & Kensley, 1969 [late Miocene to late Pliocene (Roberts & Brink 2002; Franceschini & Compton 2004)], share some characters with South America *Fissurella*, but lack the aragonitic / calcitic shell layers.

CONCLUSIONS

Fissurella (*Fissurella*) are two-layered limpets (McLean, 1984a) from intertidal and shallow subtidal habitats along the coast of western and southern South America that may well constitute a monophyletic clade (Olivares, 2006). *Fissurella* appeared abruptly on the shores of western South America by the late early Pliocene, already fully diversified into coarsely ribbed, finely ribbed, and smooth-shelled groups that are largely congruent with molecularly defined clades (Olivares, 2006). The nearly nonexistent fossil record from northern Peru and examples of Neogene immigration by western Pacific taxa to the shores of western South America favor a Southern Ocean origin for *Fissurella* (*Fissurella*), although candidates for an ancestral fissurellid taxon are not obvious; late Miocene South African *F. robusta* and *F. glarea* might serve best as sister taxa.

Fissurella limpets are ecologically important members of rocky intertidal and subtidal communities in

Peru and Chile and are abundant enough to be the target of an artisanal harvest (Castilla & Fernandez, 1998). Their sudden appearance in the region during the late Miocene or early Pliocene is likely to have had an impact on trophic dynamics in communities where medium-sized and large limpets were mostly unknown [one exception: *Cellana fuenzalida* (Herm, 1969), a giant nacellid limpet from Chile and southern Peru (Herm, 1969; Lindberg and Hickman, 1986; DeVries, unpublished data]. The interplay between recruitment of larval *Fissurella*, barnacles, and competition for space with a variety of algal species, for example, spelled out in the case of modern *F. picta* by Lopez et al. (1999), would have been repeated for an increasingly more diverse fissurellid fauna during the late early to late Pliocene, a time of global climate cooling (Ravelo et al., 2004) and mass extinction of marine mollusks in the Pliocene Peruvian Faunal Province (DeVries, 2001); opportunities for occupying new and abandoned niches may have expanded at that time.

Acknowledgments. I would like to thank Lindsey Groves (Natural History Museum of Los Angeles County, California) for the loan of comparative material from Peru, Chile, South Africa, and New Zealand; L. Groves, James McLean (also of the Natural History Museum of Los Angeles County), Javier Quinteiro (Universidad de Santiago de Compostela, Spain), Alberto Olivares (Universidad de Antofagasta, Chile), Sven Nielsen (Universität Kiel, Germany), and Robyn Stuber (United States Environmental Protection Agency, California) for their advice and help with finding relevant literature; and Mario Urbina and Marcelo Stucchi (Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru) for advice and logistical help. At various times, this research has benefited from grants from the U.S. National Science Foundation (EAR-85-03886), the Conchologists of America, Inc. (1993), and the Fulbright Senior Scholarship program (1999).

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APPENDIX

List of Locality-Samples. 'GPS' signifies field measurement with GPS position.

Yauca	Panamerican Highway, roadcut descending towards village and river valley. Late Early Pliocene.
La Mina	Beach at La Mina, Paracas Peninsula. 13°54′32″S, 76°18′58″W (Pisco 1:100,000 quadrangle). Recent.
Lomas	Intertidal rocks, beach wrack, and trash near port village of Lomas. 15°34′S, 74°49′W (Yauca 1:100,000 quadrangle). Recent.
DV 239-11	4.5 km south-southeast of Los Organos, along the Los Organos-Somatito road, cliffs near Occidental Petroleum wells 10531, 10529, and 10536. Lower 25 m of Taime Formation. Estimated coordinates 4°13′S, 81°06′30″W. Late Pliocene.
DV 401-1	Hueco La Zorra, beach. 14°02′31″S, 76°15′51″W (Punta Grande 1:100,000 quadrangle). Recent.
DV 465-1	Marine terrace north of Chala; elevation about 160–170 m above sea level. Middle Pleistocene.
DV 599-2	Montemar, Pleistocene marine terraces. 15°32′05″S, 74°47′39″W (Yauca 1:100,000 quadrangle). Middle Pleistocene.
DV 810-1	Quebrada Champeque, about 15 km north of Chala, marine terrace at 200 m above sea level. *Fissurella* specimens from surface of terrace; estimated to have been dropped by humans. Holocene.
DV 923	Knolls on southeast side of Río Acarí. 15°36′29″S, 74°37′53″W (GPS; Yauca 1:100,000 quadrangle). Early to late Pliocene. (See Figure 3.) Samples from measured section include DV 923-1 and DV 923-1e (both about 9 m) and DV 923-1a (0.2 m).
DV 1032	First curves at top of Huacllaco section. 15°52′59″S, 74°10′05″W (GPS; Chala 1:100,000 quadrangle). Includes samples DV 1032-1 (first curve in highway heading south, about 60–70 m in measured Huacllaco section, latest Pliocene) and DV 1032-2 (about 40–45 m in measured Huacllaco section, early late Pliocene). See Figure 2.
DV 1141-1	Northwest side Hueco La Zorra, beach. 14°02′46″S, 76°15′58″W (GPS; Punta Grande 1:100,000 quadrangle). Recent.
DV 1251-1	Quebrada Champeque, roadcut along Panamerican Highway. 15°48′42″S, 74°21′24″W (GPS; Chala 1:100,000 quadrangle). Late Pliocene.
DV 1254	Roadcuts along Panamerican Highway 10 km southeast of Chala, above Playa Huacllaco. 15°53′S, 74°09′W (GPS; Chala 1:100,000 quadrangle). Samples from measured section (see Figure 2) and elsewhere include: DV 1254-2 (36.5 m), DV 1254-5 (44.2 m), DV 1254-6 (41.7 m), DV 1254-10 (48 m), DV 1254-14 (41 m), DV 1254-Bal5 (27 m), DV 1254-Bal10 (47.5 m), lowest cobbles (37 m). Late early Pliocene to late Pliocene. See Figure 2.
DV 1372-1	Punta Lomas, intertidal rocks and beaches. 15°34′S, 74°49′W (Yauca 1:100,000 quadrangle). Recent.
DV 1418-1	South side Acarí depression, upper beds. 15°34′50″S, 74°36′59″W (GPS; Yauca 1:100,000 quadrangle).
DV 1628-6	Huacllaco section southeast of Chala, sandstones of upper Unit III (see Figure 2). Chala 1:100,000 quadrangle. Late Pliocene.
DV 1635-2	Yauca Depression, western side Panamerican Highway. 15°39′33″S, 75°34′54″W (GPS; Yauca 1:100,000 quadrangle). Late early Pliocene.
LACM 75-31	Intertidal zone and beach, Islota Concón, north of Viña del Mar, Chile. 32°52′S, 71°33′W. Recent. Collected by J. H. McLean, 1975.
LACM 75-32	Intertidal zone, Punta El Lacho, north of Cartagena, Chile. 33°30′S, 71°39′W. Recent. Collected by J. H. McLean, 1975.